TMESIPTERIS IN VANUATU (NEW HEBRIDES)

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ABSTRACT

Cytological, anatomical and ecological observations on *Tmesipteris* from Vanuatu are presented and attention is drawn to the variation in stem anatomy and ecology in the genus as a whole. Three species are recognised in the archipelago: *T. oblongifolia* sp. nov. (n = 104) from Tanna and Aneityum, *T. vanuatensis* sp. nov. (n = 104) from Espiritu Santo and *T. oblanceolata* (R.Br.) Desv. (n = 208) from Aneityum and Espiritu Santo.

INTRODUCTION

The genus *Tmesipteris* was based by Bernhardi (1801) on the species, *Lycopodium tannense,* which was described a year earlier by Sprengel (1800) from a Forster collection supposedly made on Tanna, Vanuatu. However, no Forster specimen from Tanna has ever been found and Sprengel's description is very brief and only sufficient to place the species in the genus. *Tmesipteris* was collected again in the archipelago by both Milne and Seeman in the middle of the last century but these collections came from Aneityum and differed from Bernhardi's description and illustration. Consequently the identity of the type species, *T. tannensis* (Spreng.) Bernh., remained for many years in doubt and our knowledge of the genus in the islands as a whole has been based on very few specimens and was inevitably incomplete.

Recently *Tmesipteris* has been found again on Tanna, Aneityum and, for the first time, on Espiritu Santo. The new material from Tanna has already clarified the typification and identity of *T. tannensis.* It differs from the species illustrated by Bernhardi (1801) and Chinnock (1976) has provided convincing evidence to show that the Forster specimen described and illustrated by Bernhardi in fact came from Dusky Sound, New Zealand, and has suggested that the reference to Tanna by Sprengel was probably an error. The Bernhardi illustration is, therefore, selected as the neotype of *L. tannense* Spreng. and the type species is now considered to be restricted to New Zealand.

The present paper gives a more complete account, including cytological and anatomical studies, of *Tmesipteris* in Vanuatu. The material from Tanna belongs to the *T. lanceolata* group and is described as a new species, *T. oblongifolia,* which is also found on Aneityum. Two further species are also recognised in the archipelago, namely, *T. vanuatensis* A.Braith. a new species proposed for material from Espiritu Santo, and *T. oblanceolata* (R.Br.) Desv. from Aneityum and Espiritu Santo.

MATERIALS AND METHODS

The material was collected by the author during the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides. The details of the localities of the collections are given in Table 1. At each locality plants were collected for herbarium specimens and preserved in 70% alcohol for anatomical studies. When available, sporangial material was also fixed in the field in 1:3 acetic-alcohol and despatched by air to the U.K. where it was stored in a deep freeze. Meiotic preparations for chromosome counts were subsequently made using the acetocarmine squash method. The material for anatomical studies was embedded in paraffin wax and the sections stained in safranin and light green or aniline blue. Spore samples were taken from dried herbarium specimens and mounted in gum chloral for measurement. Herbarium material of each species is deposited in the Herbarium, Royal Botanic Gardens, Kew.

CYTOLOGY

The results of the chromosome counts are summarised in Table 1 and representative cells are illustrated in Figs. 1 & 2. It is difficult to produce absolutely unequivocal counts in the genus because of a) the high chromosome numbers, b) variation in the size of chromosomes and c) the sometimes peculiar shapes of the bivalents. The latter has generally been attributed to a laxity in the spiral structure (Manton 1950, Lovis 1977). Nevertheless the counts listed in Table 1 are accurate to within one or two chromosomes except where indicated, and even in these cases the order of the chromosome number is not in doubt.

TABLE 1. Chromosome Numbers in *Tmesipteris* from Vanuatu

Species	Locality	Chromosome number	Spore length* (μm)	Length of Stomata* (μm)
T. oblongifolia	RSNH 2146, Woptiabo, Aneityum	n = 104	62.7 ± 4.2	96.0
	RSNH 2204, Mt. Toukosmeru, Tanna	n = 104	57.5 ± 3.3	92.5
	RSNH 2211, Mt. Toukosmeru, Tanna	n = 104	57.4 ± 3.8	—
T. vanuatensis	RSNH 2354, Apouna Valley, Espiritu Santo	n = 104	62.0 ± 3.6	93.2
	RSNH 2382, Mt. Tabwemasana, Espiritu Santo	n = c.104	58.6 ± 3.6	92.3
T. oblanceolata	RSNH 2112, Inrero, Aneityum	n = 208	82.8 ± 4.1	133.4
	RSNH 2152, Nezwon Nelgon, Aneityum	n = c.208	81.5 ± 4.3	123.6

* Data based on 100 measurements from one specimen from each collection.

The numbers recorded here fall into the cytological pattern already established for the genus by Barber (1957) from Australian material of two groups with n = 104 and n = 208 respectively. These relatively high numbers have in the past been designated as various levels of polyploidy but are here interpreted in terms of the lowest extant number known in the Psilotales, which is n = 52 (Lovis 1977). Thus *T. oblongifolia* and *T. vanuatensis* are tetraploids and *T. oblanceolata* is an octoploid.

The mean length of spores and stomata are also given in Table 1. It is clear from this data that the spores and stomata of the octoploid, *T. oblanceolata,* are considerably larger than those of the tetraploids, *T. oblongifolia* and *T. vanuatensis.* Although the samples are small, the data do suggest that these microcharacters are potentially useful in Vanuatu as polyploid indicators.

ANATOMY

The species from Vanuatu show the basic vascular pattern described from other *Tmesipteris* species (Sykes 1908, Sahni 1925). Thus the solid core of tracheids in the rhizome becomes medullated and breaks up in the transition region to form a variable number of groups of tracheids arranged around a central pith. The representative sections illustrated in Fig. 3 show the typical arrangement of the stele at the top of the transition region. In all three species groups of tracheids can be seen surrounding a well defined pith. There are, however, differences in the nature of the pith cells and two basic types can be recognised.

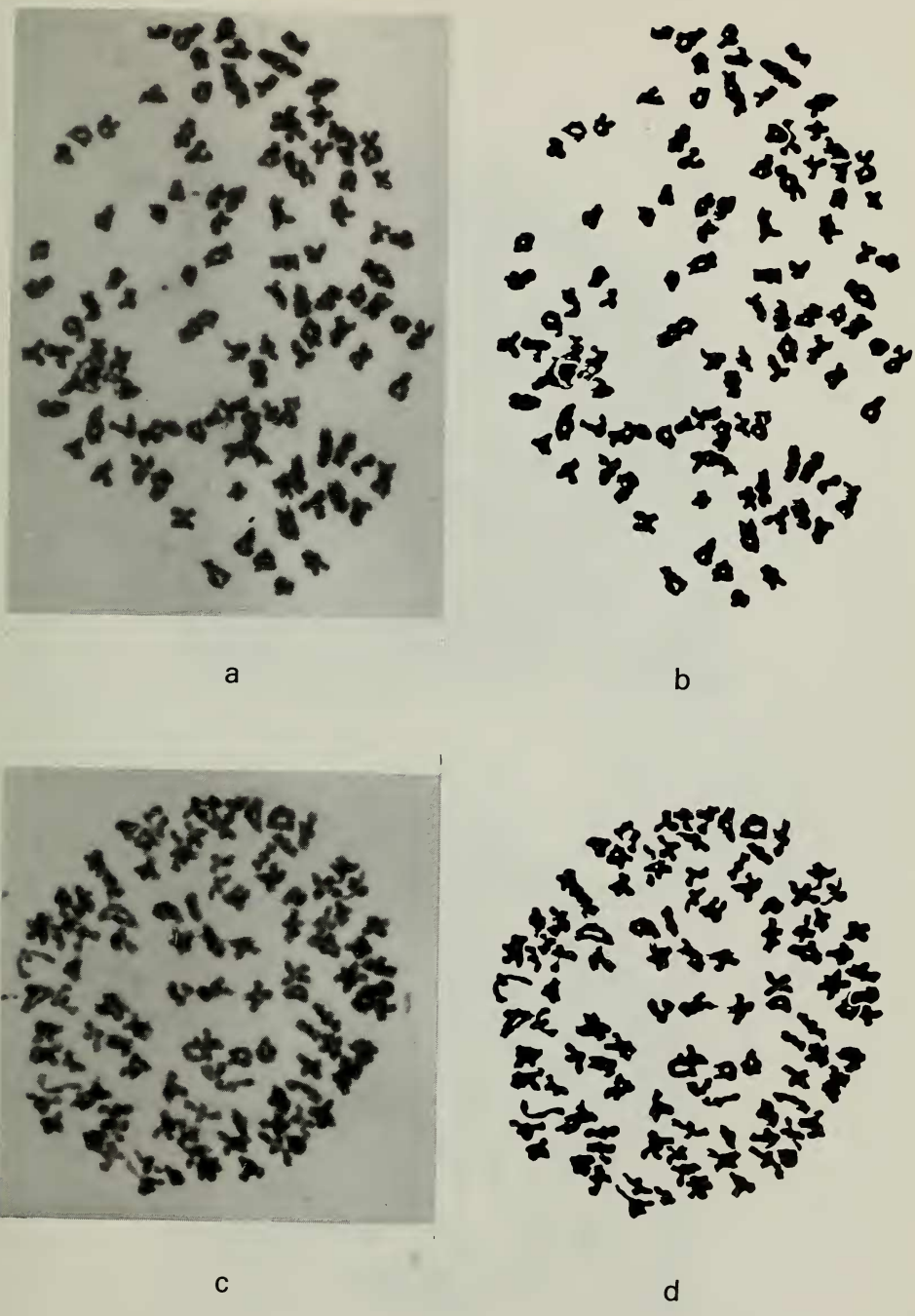
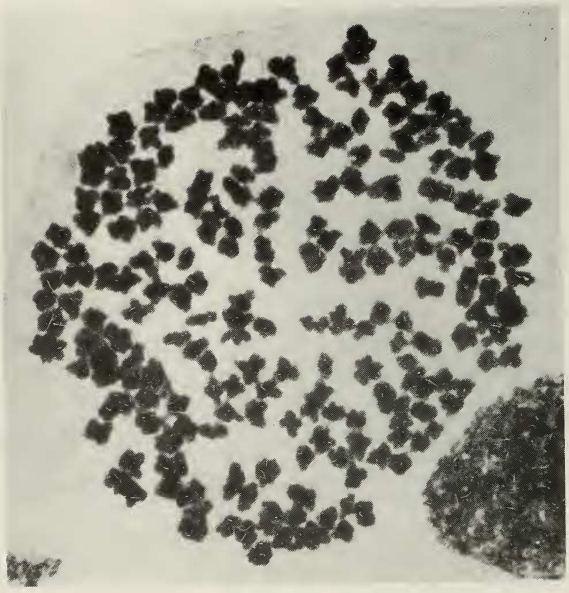


FIGURE 1. Permanent acetocarmine preparations for meiosis. X 750. a) *T. oblongifolia* RSNH 2204. b) Explanatory diagram showing 104 bivalents. c) *T. vanuatensis* RSNH 2354. d) Explanatory diagram showing 104 bivalents.

a



b

FIGURE 2. Permanent acetocarmine preparation of meiosis. X 750. a) *T. oblanceolata* RSNH 2112. b) Explanatory diagram showing 208 bivalents.

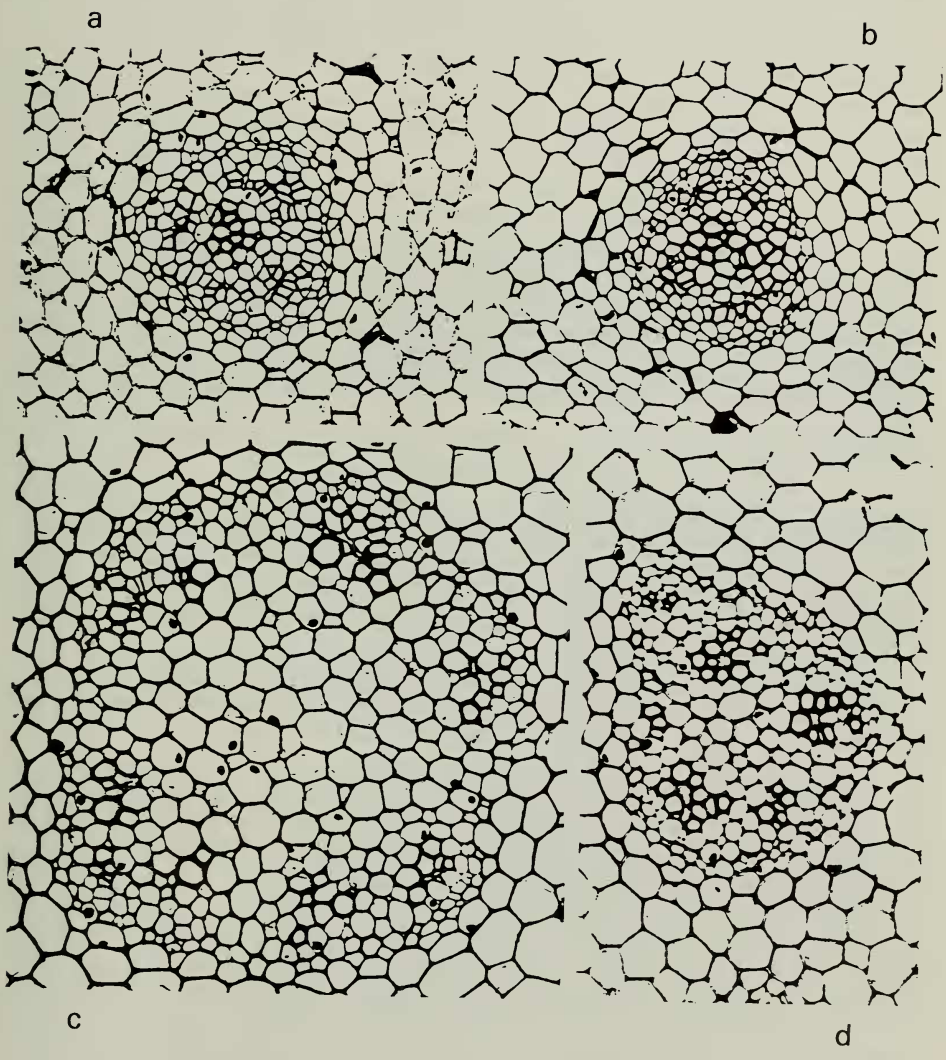


FIGURE 3. Transverse sections of aerial shoots of *Tmesipteris* species from Vanuatu. X 100. a) *T. oblongifolia* RSNH 2204. b) *T. vanuatensis* RSNH 2382. c) & d) *T. oblanceolata* RSNH 2112. a, b & c from top of transition region; d from distal part of aerial shoot.

The first type is illustrated by *T. oblongifolia* (Fig. 3a) and *T. vanuatensis* (Fig. 3b). In these species the pith is small and made up of narrow thick walled, lignified cells which in transverse sections have the same appearance as fibres or sclerenchyma. The tracheids around the pith are by contrast thinner walled and the tracheid bundles can be located in the sections by their mesarch protoxylem. The second type of pith is characteristic of *T. oblanceolata* (Fig. 3c,d). Here the groups of tracheids surround a relatively large pith made up of thin walled parenchymatous or slightly collenchymatous cells. Even in the distal parts of the leafy shoot, where the number of tracheid bundles and pith are much reduced, the pith cells are still essentially parenchymatous (Fig. 3d). Medullary xylem has been found associated with this type of pith in *T. vieillardii* (Sahni 1925) from New Caledonia and *T. oblanceolata* (Braithwaite 1973) from the Solomon Islands, but none has been found in the material from Vanuatu. On present evidence the pith type appears to be constant for each species.

Variations in the pith cells in the stems of other *Tmesipteris* species have been reported by a number of previous investigators, notably Dangeard (1890-91), Sahni (1925) and Braithwaite (1973). In all cases two types of pith composed of either parenchymatous cells or sclerenchymatous cells have been recognised. The consistency of the observations so far suggests that this recently rather neglected anatomical character perhaps merits further investigation to establish whether it may be useful as a taxonomic indicator, either at the species level or for the grouping of species.

ECOLOGY AND DISTRIBUTION

During the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides *Tmesipteris* was encountered only sporadically in montane forest at altitudes of 475-745m on Aneityum and Tanna in the south and 900-1650m on Espiritu Santo in the north. However, many of the other larger islands in the group attain altitudes in excess of 500m so that it can perhaps be anticipated that further collecting will extend its distribution within the islands.

T. oblongifolia and *T. vanuatensis* were confined almost exclusively to the lower parts of the tree fern trunks belonging to the genus *Cyathea.* Both species were recorded from *C. lunulata,* but they were also collected from other *Cyathea* species so that they do not appear to be confined to any particular species.

Unlike the other two species, *T. oblanceolata* was never found on tree ferns. It grew among mosses and filmy ferns on the trunks of angiospermous trees such as *Metrosideros* and *Weinmannia* (see Fig. 1b in Braithwaite 1975) or out of organic accumulations beneath epiphytic ferns such as *Asplenium nidus. T. oblanceolata* has also been recorded on decayed wood on the forest floor (Milne 272K). Non-tree-fern substrates have been reported for *Tmesipteris* species elsewhere; notably *T. vieillardii* of New Caledonia (Sahni 1925), *T. tannensis* (Spreng.) Bernh. s. strict. in New Zealand (Chinnock 1976) and *T. oblanceolata* from the Solomon Islands (Braithwaite 1973).

It is becoming increasingly clear that speciation within the genus has been accompanied by some ecological differentiation, although the extent to which the latter may be useful in delimiting species or determining species relationships is at present not clear.

KEY TO THE SPECIES

Aerial shoots 6-16cm long, leaves ovate-oblong or narrowly oblong to elliptic.

Leaves ovate-oblong with obtuse apices, l/b ratio <3, distichously arranged beyond the sporophylls. *T. oblongifolia*

Leaves narrowly oblong to elliptic with acute apices, l/b ratio >3, spirally arranged beyond the sporophylls. *T. vanuatensis*

Aerial shoots 15-38cm, leaves narrowly rectangular to narrowly obovate with truncate or rounded apices. *T. oblanceolata*

Tmesipteris oblongifolia A. Braith. **sp. nov.**

Planta epiphytica in truncis filicum arborum. Surculis aerius simplex, pendulus, (6-)8-14(-16)cm longus, per unum crescentem maturescens, folio magno terminati. Folia infra sporophylla spiraliter disposita, supra sporophylla disticha disposita, subcoriacea, (7-)9-13(-15)mm longa, (3-)3.5-4.5(-5)mm lata, ovato-oblonga, apicibus rotundatis obtusis mucronatis. Sporophylla spiraliter disposita, medianum caulis foliosi occupantes, longitudine folia aequantia. Synangium 2-4mm longum, sporangiis lobiis aequalibus. Sporae bilaterales, monoletae, concavo-convexae, (51-)57-62(-73)µm longae, (18-)21-22(-25)µm latae. Chromosomatum numerus gametophyticae 104.

Holotype: Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 500m, epiphyte on *Cyathea* trunk (same sp. as RSNH 2184), 28 Jul. 1971, A.F. Braithwaite RSNH 2204 (K).

Plant epiphytic on trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-14(-16)cm long, maturing in one growing season and terminating in large leaf-like appendage. Leaves spirally arranged below the sporophylls, distichously arranged in portion of leafy shoot distal to the sporophylls, 3-4 per cm stem, subcoriaceous, (7-)9-13(-15)mm long, (3-)3.5-4.5(-5)mm wide, ovate-oblong with rounded obtuse mucronate apex. Sporophylls spirally arranged, 5 per cm stem, occupying the middle of the leafy part of the shoot or throughout the upper two thirds, ± equal in length or slightly shorter than the leaves. Synangia 2-4mm long, 1-1.5mm high, with lobes of sporangia approximately equal, ± globular. Spores bilateral, monolete, concavo-convex, (51-)57-62(-73)µm long, (18-)21-22(-25)µm broad. Chromosome number n = 104.

T. oblongifolia is closely allied to *T. lanceolata* from New Caledonia and New Zealand. The two species are similar in size and share a distichous arrangement of leaves in that portion of the leafy shoot distal to the sporophylls. The two species also possess the same pith type in the stem and chromosome number. Dangeard (1890-91) describes and illustrates the pith cells of *T. lanceolata* as "fibres medullaires" and unpublished chromosome counts by the author show it to be a tetraploid. *T. oblongifolia* can however be distinguished by its thinner texture, ovate-oblong leaves with an obtuse apex and by the position of the sporophylls, which are found in the middle or upper two thirds of the leafy shoot and never only at the base or in the lower half as in *T. lanceolata*.

Distribution: Philippines, Vanuatu and the Marquesas.

Specimens examined:
VANUATU. Aneityum, ridge leading to Woptiabo, c.5km ENE of Anelcauhat (20°13'S 169°49'E), 487m, epiphytic on *Cyathea lunulata* in ridge side forest, 23 Jul. 1971, Braithwaite RSNH 2146 (K). Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 644m, epiphytic on base of large *Cyathea lunulata,* 28 Jul. 1971, Braithwaite RSNH 2211 (K).
MARQUESAS. Feani, vieux sentrer 'Atuona à Hanamenu, haute vallée côte Hanamenu, 850m, brousse fougeres arborescentes et *Freycinetia,* épiphyte sur les bases de fougeres arborescentes, assay rare, 5 Mar. 1975, Schafer & Oline 5272 (K);

Chemin d'Omoa à Hanavave, crête principale, mont Moratina (Mt. Bóise de la carte), 670m, brousse assay humide avec *Cyathea, Crossostylis,* sur bases de *Cyathea,* assay rare, 18 Sept. 1975, Schafer 5758 (K); Feani, montagnes entre la haute vallée de Hanamenu et la crête de Temetiu, 900m, petit haut vallée à foret très humide: *Crossostylis, Cyathea, Pandanaceae, Weinmannia, Myrsine,* sur troncs de *Cyathea,* assay rare, 23 Oct. 1975, Schafer 5914 (K); Nukuhiva, Quayle 1305 (K).
PHILIPPINES. Mindanao, Davao Dist: Mt. Apo 6000ft, epiphyte always on trunks of tree ferns, Oct. 1904, Copeland 1433 (K); Mt. Apo, May 1909, Elmer 10600 (BM, K); Mt. Apo, 9000ft, Feb. 1929, Hachisaka s.n. (BM); Mt. Apo, 1800m, 1932, Copeland 203 (BM).

Tmesipteris vanuatensis A. Braith. **sp. nov.**

Planta epiphytica in truncis filicum arborum. Surculis aerius simplex, pendulus, (6-)8-15(-16)cm longus, foliis et sporophyllis spiraliter dispositis et folio magno terminatis. Folia subcoriacea, 8-14mm longa, 2.5-3.5mm lata, anguste oblonga vel anguste elliptica, apicibus acutis et mucrone setaceo 0.5-1.0mm longo. Sporophylla medianum caulis foliosi occupantes, longitudine folia subaequantia. Synangium parvum, 3-3.5mm longum, globosum, sporangiis lobis aequantibus. Sporae monoletae, concavo-convexae, (50-)59-62(-67)µm longae, (18-)21(-25)µm latae. Chromosomatum numerus gametophyticae 104.

Holotype. Espiritu Santo, crest of NW ridge of Mt.Tabwemasana, c. 1600m, epiphyte on *Cyathea* sp. in ridge top *Metrosideros-Weinmannia* forest, 2 Sept. 1971, A.F. Braithwaite RSNH 2382 **(K).**

Plant epiphytic on the trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-15(-16)cm long, maturing in one growing season, with leaves and sporophylls spirally arranged and terminating in a large leaf-like appendage. Leaves subcoriaceous, 8-14mm long, 2.5-3.5mm, narrowly oblong or ovate-oblong to narrowly elliptical with acute apices and bristle-like mucro 0.5-1.0mm long. Sporophylls occupying the middle or throughout leafy part of shoot, equal to or slightly shorter than the leaves. Synangia 3-3.5mm long, globose, persistent, with two equal sporangial lobes. Spores monolete, concavo-convex, (50-)59-62(-67)µm long, (18-)21(-25)µm broad. Chromosome number n = 104.

T. vanuatensis can be distinguished from *T. oblongifolia* by its spirally arranged narrowly oblong to almost elliptical leaves with a larger length/breadth ratio and generally acute apices. The leaves are also more widely spaced and arise from the stem at a more acute angle giving the plant a generally more lax and slender appearance than *T. oblongifolia* (Fig. 4).
Known only from Mt. Tabwemasana, Espiritu Santo.

Other specimen examined:
Espiritu Santo. Camp site no. 4, Nokovula Village, 23k SSW of Malau, Big Bay (15°20'S 166°44'E), disturbed forest area below village, c. 900m, epiphyte on *Cyathea lunulata,* 1 Sept. 1971, Braithwaite RSNH 2354 (K).

Tmesipteris oblanceolata Copel., Philip. J. Sci. 60: 99 (1936); A. Braith., Brit. Fern Gaz. 10: 296 (1973).

Type: Solomon Islands, Guadalcanal, Tutuve Mt, 1700m, Kajewski 2632 (A).

Plants epiphytic on angiospermous tree trunks or growing on moss covered decaying wood on forest floor. Aerial shoots simple, pendulous or occasionally sub-erect, (15-)20-30(-38)cm long, maturing in a single growing season and terminated by a small leaf-like appendage; transition region (4-)5-10(-11)cm long; leaves and sporophylls spirally arranged and often tending to decrease in size towards the apex. Leaves (10-)11-14(-16)mm long, 2.5-3.5mm broad, coriaceous to subcoriaceous, (4-)5(-6) per cm stem, narrowly oblong or rectangular but narrowing towards the base to narrowly obovate, ± falcate, apex truncate and sometimes bilobed to rounded, mucronate; mucro stiff, 1-2mm long. Sporophylls developed in mid region or throughout upper two thirds of leafy shoot, equal in length to leaves; synangia 3-4mm long, 1.5-2mm high, persistent, bilocular, sporangial lobes ± equal. Spores monolete, concavo-convex, (73-)81-83(-94)µm long, (25-)31(-36)um broad. Chromosome number n = 208.

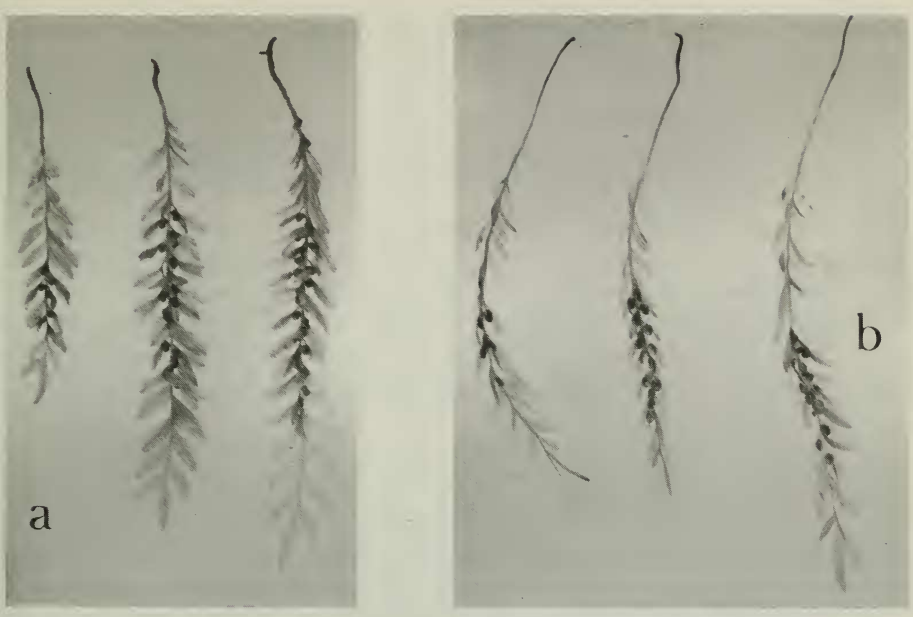


FIGURE 4. a) *T. oblongifolia* RSNH 2204. b) *T. vanuatensis* RSNH 2382. Specimens preserved in alcohol. X 1/2.

T. oblanceolata in Vanuatu is rather variable with respect to length of the aerial shoot and in size and shape of the leaves. The plants from Espiritu Santo with aerial shoots up to 26cm long bearing short narrowly obovate leaves with rounded apices, are virtually indistinguishable from *T. oblanceolata* Copel. from the Solomon Islands, except that medullary xylem found in specimens from the Solomon Islands (Braithwaite 1973) was not found in the single specimen available for sectioning from Espiritu Santo. The pith is otherwise of a similar parenchymatous type. The more extensive collections from Aneityum have aerial shoots up to 38cm long, some possessing narrow slightly obovate leaves with rounded apices, while the majority have longer, narrowly rectangular leaves with truncate apices. Similar variation is evident in material attributed here to *T. oblanceolata* from New Caledonia and Samoa.

The plants from Aneityum, with leaves with markedly truncate sometimes almost bilobed apices, are very similar to the Australian species *T. truncata* (R.Br.) Desv. They also share the same chromosome number. Barber (1957) reported a chromosome number of n = 201-211 for *T. truncata* from several different localities in New South Wales and n = 208 has been found here in material from Aneityum. There are however some ecological and anatomical differences. The plants from Aneityum are either epiphytic on angiospermous trees or terrestrial on decayed wood while *T. truncata* from Australia is generally, though not exclusively, epiphytic on tree ferns. There are two specimens from Australia at Kew collected from non-tree-fern substrates; one with typical truncate leaves labelled "Macquarie Harbour, humid rocky banks B mountains in shaded woods, 1825, Cunningham 92"; and the other with more oblanceolate leaves labelled "Head of Clyde River, 25 miles SSW of Howra, 2000ft, on mossy ledge of sandstone cliff, 2 May 1937, Rodway 2369". The anatomical difference concerns the pith type in the stem. Dangeard (1890-91) reported a sclerenchymatous

pith type in *T. truncata* from Australia which differs from the parenchymatous pith found here in the material from Vanuatu. However Dangeard (in contrast to the often very detailed drawings from the stems of the other species he examined) shows only a very small outline tissue sketch for the stem of *T. truncata* (Plate XIV, Fig. 11) and it would be desirable to have the detail confirmed for material both from tree-fern trunks and from non-tree-fern substrates. It is possible that variation in the pith type may be correlated with differences in ecology.

T. oblanceolata and *T. truncata* are clearly very closely related and they probably represent forms of the same species. However on present evidence it is difficult to assess the extent or taxonomic significance of their ecological and anatomical differences. Future studies may well confirm their conspecificity but it is considered preferable for the time being to segregate the Pacific material under *T. oblanceolata*.

Distribution: New Caledonia, Vanuatu, Solomon Islands, Fiji, Samoa.

Specimens examined:
VANUATU. Aneityum: ridge crest N of Woptiabo, S end of Nithuon Nelvau (20°13'S 169°49'E), 640m, ridge top forest with *Metrosideros,* epiphytic on large leaning tree on ridge top growing underneath a large plant of *Asplenium nidus,* 23 Jul. 1971, Braithwaite RSNH 2152 (K); c. 5km NE by N of Anelcauhaut, on crest of ridge running S from Inrero (20°11'S 169°47'E), 745m, epiphytic on trunk of *Metrosideros,* occasionally on forest floor, 21 Jul. 1971, Braithwaite RSNH 2112 (K); high grounds, decayed trees, Nov. 1853, Milne 272 (K); 1854, Seeman s.n. (BM); crête S de l'Inrero, alt. 750m, epiphyte au bas de troncs, fronde portee ± horizontalement, 23 Jul. 1971, Raynal RSNH 16147 (K). Espiritu Santo: northern ridge of Mt. Tabwemasana (15°22'S 166°45'E), 1650m, low forest on ridge crest, *Weinmannia* dominant, 4 Sept. 1971 Raynal RSNH 16386 (P).
SOLOMON ISLANDS. Guadalcanal, Mt. Popomanaseu, halfway between upper camp and Vunuvelakama, c. 5000ft, growing erect in moss around base of trees in ridge top moss forest, 3 Nov. 1965, Braithwaite RSS 4782 (K).
NEW CALEDONIA. Mt. Koghi, kauri ft. 1000ft, on prostrate decaying trunk covered with liverworts, 13 Jun. 1914, Compton 764 (BM).
LORD HOWE ISLAND. Epiphyte on the top of Mt. Gower in mist forest, 2600ft, Aug. 1965, Game 65/1/SN (K).
SAMOA. May 1876, Whitmee s.n. (K).

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